

HOST AND ELEVATIONAL SPECIFICITY OF PARASITIC BEETLES (*AMBLYOPINUS* SOLSKY) (COLEOPTERA: STAPHYLINIDAE) IN PANAMA

Robert M. Timm and James S. Ashe

Abstract.—The literature on staphylinid beetles of the tribe Amblyopinini, all of which are parasitic on Neotropical or Australian mammals, has provided few specifics on the natural history and host relationships of these beetles. We provide the first comprehensive data on host relationships and elevational range for a community of amblyopinines and their potential hosts. Mammals collected from eight separate localities along an elevational transect ranging from 900 to 1856 m were examined for parasitic beetles of the genus *Amblyopinus*. At these localities, mammals collected include a diverse array of marsupials, edentates, insectivores, bats, rodents, and lagomorphs. Among these potential hosts, parasitic beetles were limited to a subset of the cricetine rodents. Amblyopinines were collected from only two species of rodents at two localities with elevations of 1425–1525 m and 1800–1825 m. *Amblyopinus emarginatus* Seevers was collected at both localities, where it was found on a single species of host, *Oryzomys albigularis*. In contrast, *A. tiptoni* Barrera was collected only at the higher elevation on *Reithrodontomys creper*. These data, as well as re-analysis of literature records, are consistent with the interpretation that these beetles are much more host restricted than has been previously recognized. Additionally, while these beetles appear to be tracking specific species of hosts, they are restricted to that subset of the hosts' range above 1000 m. This implies that factors other than host range are of considerable importance to the distribution and ecology of these beetles.

Staphylinid beetles of the tribe Amblyopinini have most often been collected from the fur of mammals. They are thought to be parasitic, although there is little information available on the natural history of this tribe.

There are five genera in the tribe Amblyopinini, four of which are restricted to the Neotropical region, *Amblyopinus* Solsky, *Amblyopinodes* Seevers, *Edrabius* Fauvel, and *Megamblyopinus* Seevers, and a single genus, *Myotyphlus* Fauvel, which occurs in Australia and Tasmania (Seevers 1955). Members of the Amblyopinini are primarily found at high elevations and are seldom reported on mammals collected below 1000 meters elevation. All four Neotropical gen-

era are found in South America; members of only one genus, *Amblyopinus*, are found in Central America and Mexico. Thirty-four species of *Amblyopinus* currently are recognized, most being known by only a few specimens with little biological data available. Five species of *Amblyopinus* are known from Central America and Mexico (*A. bolivari* Seevers and *A. isabellae* Barrera from Mexico, *A. schmidti* Seevers from Guatemala, *A. tiptoni* Barrera from Costa Rica and Panama, and *A. emarginatus* Seevers from Panama, Colombia, and Venezuela).

The most common hosts are cricetine rodents, although a wide range of hosts has been reported and includes marsupials; caviomorph, myomorph, and sciuriform

rodents; a sloth; and bats. Of the Panamanian amblyopinines, *A. tiptoni* has been collected most commonly on *Peromyscus nudipes* (Barrera 1966a, b), though it has also been reported on *Reithrodontomys creper* (Barrera 1966a, Vaughan 1982). In contrast, *A. emarginatus* has been reported from a wide array of hosts, though most commonly from species of *Oryzomys* (Barrera and Machado-Allison 1968, Machado-Allison and Barrera 1972).

The purpose of this paper is to report new data available for two species of *Amblyopinus* in Panama, *A. emarginatus* and *A. tiptoni*. We are now able to provide detailed information on host and elevational specificity of these species. Additionally, we examined specimens previously reported from Panama and provide a reevaluation of this material.

Materials and Methods

From 15 May through 10 July 1980, Ronald H. Pine and Robert J. Izor collected small mammals and their ectoparasites in the Cerro Colorado region of western Panama. Mammals were collected at eight localities ranging from 900 to 1856 m (see Pine and Handley, in prep.). Localities where *Amblyopinus* was encountered include (Fig. 1): Panama, Chiriquí-Bocas del Toro boundary, Cerro Bollo, 3.5 km E of Escopeta, 1800–1856 m (subsequently referred to as the “Cerro Bollo” locality). Originally cloud forest and elfin woodland, considerable forest remains, though some clearing has been undertaken for surveying purposes. Traps were set along pre-existing paths and paths cut through the forest for the trapline.

Species of small mammals taken at Cerro Bollo (numbers collected in parentheses) include: Talamancan small-eared shrew, *Cryptotis gracilis* (1); blackish small-eared shrew, *Cryptotis nigrescens* (15); *Cryptotis* sp. (1); Tomes’ rice rat, *Oryzomys albigularis* (14); cloud forest pygmy rice rat, *Oryzomys*

vegetus (3); Chiriquí harvest mouse, *Reithrodontomys creper* (33); Mexican harvest mouse, *Reithrodontomys mexicanus* (2); and Chiriquí brown mouse, *Scotinomys xerampelinus* (9) (Pine and Handley, in prep.).

Bocas del Toro, 25 km NNE of San Felix, 1425–1525 m (subsequently referred to as the “San Felix” locality). This area is cloud forest, except where disturbed. Trapping took place along a recently cut trail and a small stream, the Quebrada Alicia.

Species of small mammals taken at this locality (numbers collected in parentheses) include: opossum, *Didelphis marsupialis* (1); South American mouse-opossum, *Marmosa robinsoni* (2); blackish small-eared shrew, *Cryptotis nigrescens* (5); Tomes’ rice rat, *Oryzomys albigularis* (50); cloud forest pygmy rice rat, *Oryzomys vegetus* (2); naked-footed deer mouse, *Peromyscus nudipes* (15); and Mexican harvest mouse, *Reithrodontomys mexicanus* (9) (Pine and Handley, in prep.).

Other species of terrestrial small mammals collected at lower elevations (900, 1275–1325, and 1400–1425 m) include: water opossum, *Chironectes minimus*; two-toed sloth, *Choloepus hoffmanni*; forest rabbit, *Sylvilagus brasiliensis*; Harris’ rice rat, *Oryzomys aphrastus*; pygmy rice rat, *Oryzomys fulvescens*; yellow deer mouse, *Peromyscus flavidus*; and hispid cotton rat, *Sigmodon hispidus*. Additionally, 19 species of bats were collected throughout the elevational range (Pine and Handley, in prep.). None of these other mammals were parasitized by *Amblyopinus*, nor were any *Amblyopinus* found below 1425 m elevation.

An attempt was made to collect every beetle encountered, although a small number escaped. The actual number that escaped is uncertain, but represents only a very small percentage of those captured. None of the beetles which escaped were from hosts or elevations which differ from those reported here (R. Izor and R. Pine, pers. comm.). Thus, these data provide an informative representation of beetle distribu-

tions among available hosts and elevational range at these localities.

The mammals collected are deposited at the U.S. National Museum of Natural History in Washington; beetles at the Field Museum of Natural History.

Results

Staphylinids of the genus *Amblyopinus* were collected at two localities in Panama, the San Felix locality and the Cerro Bollo locality. Two species of *Amblyopinus* were collected. *Amblyopinus emarginatus* was obtained at both localities, although it was common at only 1425–1525 m. *Amblyopinus tiptoni* was obtained at only 1800–1856 m. These two localities are separated by a distance of less than 3 km.

Amblyopinus emarginatus SeEVERS

Amblyopinus emarginatus was taken from a single host species, Tomes' rice rat *Oryzomys albigularis*, from two elevational ranges (1425–1525 m and 1800–1856 m). It was collected from ten hosts; nine from the lower elevational range (total of 29 beetles) and one from the higher (1 beetle). In the lower elevational range (1425–1525 m) 50 *O. albigularis* were trapped, 35 males and 15 females. Of these, 9 had beetles (Table 1), 8 males and 1 female. At the higher elevation (1800–1856 m) 14 *O. albigularis* were trapped, 10 males and 4 females. Only 1 male had specimens of *A. emarginatus* (Table 1). At the San Felix locality, beetles were taken between 22 May and 11 June 1980; at the Cerro Bollo locality, the single *A. emarginatus* was taken on 7 July 1980.

Specimens of *A. emarginatus* from these localities were compared with the holotype of *A. emarginatus* from Colombia in the collection of the Field Museum of Natural History and found to be well within the expected range of variation in structural features for this species. The specimens of *A. emarginatus* from western Panama are isolated from the other populations of this

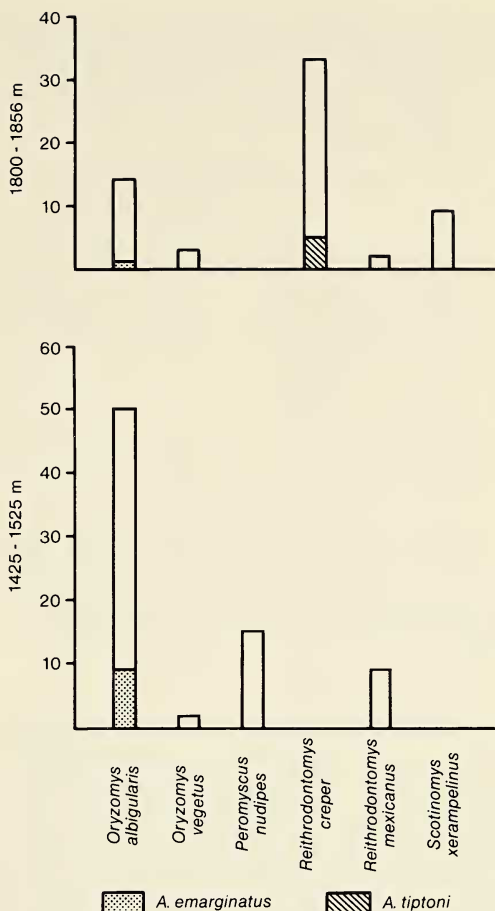


Fig. 1. Numbers of individuals of mammal species captured (total bar) and corresponding numbers from which specimens of *Amblyopinus emarginatus* SeEVERS and *Amblyopinus tiptoni* BARRERA were collected from two localities (Cerro Bollo, 3.5 km E of Escopeta, 1800–1856 m; and Bocas del Toro, 25 km NNE San Felix, 1425–1525 m) along an elevational transect in Panama. We follow Pine (pers. comm.) in recognizing *Oryzomys vegetus* as distinct from *O. fulvescens*.

species in the highlands of Columbia and Venezuela by about 900 km of the Panamanian and northwestern Colombian lowlands.

Amblyopinus tiptoni BARRERA

Amblyopinus tiptoni was found on only one species of host, the Chiriquí harvest mouse, *Reithrodontomys creper*, at only one

Table 1.—Numbers of specimens of *Amblyopinus emarginatus* collected at two localities in western Panama [Cerro Bollo, 3.5 km E of Escopeta (=“Cerro Bollo” locality); Bocas del Toro, 25 km NNE of San Felix (=“San Felix” locality)] from individual specimens of *Oryzomys albigularis*.

| Host Catalog No.* | Locality | No. beetles | | |
|-------------------|-------------|-------------|----------|-------|
| | | Males | Fe-males | Total |
| 541126 | San Felix | — | 2 | 2 |
| 541127 | San Felix | 5 | 5 | 10 |
| 541131 | San Felix | 1 | 2 | 3 |
| 541135 | San Felix | 1 | 1 | 2 |
| 541136 | San Felix | — | 1 | 1 |
| 541141 | San Felix | 1 | 2 | 3 |
| 541142 | San Felix | 3 | 1 | 4 |
| 541354 | San Felix | 2 | — | 2 |
| 541373 | San Felix | — | 2 | 2 |
| 541356 | Cerro Bollo | — | 1 | 1 |
| Totals | | 13 | 17 | 30 |

* Host Catalog No. refers to the catalog number of mammal specimens housed at the Smithsonian Institution.

elevation range, 1800–1856 m. This was the only locality trapped at this high an elevation, and the only locality where *R. creper* was obtained. *Amblyopinus emarginatus* was also taken here, but is represented by only a single individual. Sixteen males and 16 females of *R. creper* were trapped, including all age categories. A total of seven specimens of *A. tiptoni* were found on 5 of these (Table 2), 2 males and 3 females. *Amblyopinus tiptoni* was collected between 15 and 22 June 1980.

Discussion

a) *Host specificity*.—In this study 38 species of small mammals were collected and surveyed for parasitic arthropods over an eight week period in western Panama. This included 19 terrestrial species and 19 species of bats. Of these potential hosts, *Amblyopinus emarginatus* was found only on *Oryzomys albigularis* and was present only at the two localities (and elevations) where *O. albigularis* was trapped. *Amblyopinus tiptoni* was found only on a single

Table 2.—Numbers of specimens of *Amblyopinus tiptoni* collected at one locality in western Panama [Cerro Bollo, 3.5 km E of Escopeta (=“Cerro Bollo” locality)] from individual specimens of *Reithrodontomys creper*.

| Host Catalog No.* | Locality | No. beetles | | |
|-------------------|-------------|-------------|----------|-------|
| | | Males | Fe-males | Total |
| 541206 | Cerro Bollo | 1 | 2 | 3 |
| 541212 | Cerro Bollo | 1 | — | 1 |
| 541220 | Cerro Bollo | — | 1 | 1 |
| 541225 | Cerro Bollo | 1 | — | 1 |
| 541227 | Cerro Bollo | 1 | — | 1 |
| Totals | | 4 | 3 | 7 |

* Host Catalog No. refers to the catalog numbers of mammal specimens housed at the Smithsonian Institution.

species of host, *Reithrodontomys creper*, at the single locality and elevational range where *R. creper* was trapped.

Several thousand specimens of mammals were collected from throughout Panama as part of the zoonoses surveys by the Gorgas Memorial Laboratory and the “Ectoparasites of Panama” surveys during the 1950’s and 1960’s. Most of the 201 species of native terrestrial mammals listed by Handley (1966) from Panama have been examined for ectoparasites. During these surveys, only three specimens of *Amblyopinus emarginatus* were obtained, all from a single locality at 1525 m in Bocas del Toro Province. Two species of hosts were reported, *Oryzomys albigularis* and *Peromyscus nudipes*.

Elsewhere, *A. emarginatus* has been collected on a number of occasions from the highlands of Colombia and Venezuela. Throughout the range of *A. emarginatus*, it has been reported from a variety of mammals including: *Oryzomys albigularis*, *O. caliginosus*, *O. alfaroi*, *O. concolor*, *O. devius*, *Akodon urichi*, *Peromyscus flavidus*, *Rhipidomys venustus*, *Thomasomys fuscatus*, *T. laniger*, and *T. sp.*; as well as from *Didelphis marsupialis*, *Marmosa dryas*, *Bradypus infuscatus*, *Myotis nigricans*, and *Vampyrops oratus* (Seevers 1955; Macha-

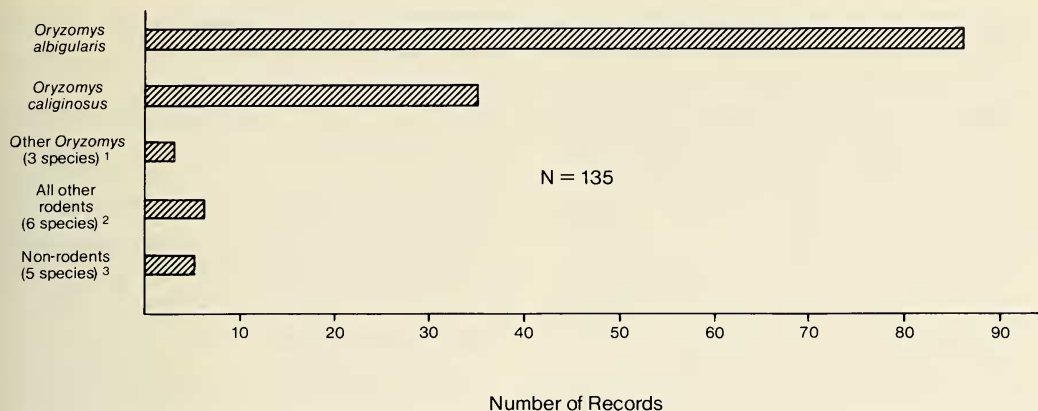


Fig. 2. Numbers of host individuals from which *Amblyopinus emarginatus* Seevers has been recorded, compiled from literature citations (Seevers 1955; Machado-Allison and Barrera 1964, 1972; Barrera 1966a, b; Barrera and Machado-Allison 1968).

¹ *O. alfaroi*, *O. concolor*, *O. devius* (*O. devius* is often considered conspecific with *O. albigularis*).

² *Akodon urichi*, *Peromyscus flavidus*, *Rhipidomys venustus*, *Thomasomys fuscatus*, *T. laniger*, and *Thomasomys* sp.

³ *Didelphis marsupialis*, *Marmosa dryas*, *Bradypus infuscatus*, *Myotis nigricans*, and *Vampyrops oratus* (these records must be considered suspect).

do-Allison and Barrera 1964, 1972; Barrera 1966a; Barrera and Machado-Allison 1968). The last five of these, which include all reports from marsupials, the sloth, and bats, represent single records and should be considered suspect. The records from the two bats were even suspected to be contaminations in the original report by Machado-Allison and Barrera (1972). Among literature records of *A. emarginatus* ($n = 135$) (Fig. 2), most reports have been from species of *Oryzomys* (124; 91.9%), and the large majority of these have been either from *O. albigularis* ($n = 86$; 69.4%) or *O. caliginosus* ($n = 35$; 28.2%). All other host records represent single reports. This strongly suggests that species of *Oryzomys* represent the primary hosts of *A. emarginatus*.

Most records of *A. emarginatus* from *Oryzomys* are from *O. albigularis*, and indeed it has been reported from this host throughout the known range of the beetle. However, at one locality in Colombia, *A. emarginatus* was commonly reported from *O. caliginosus* (Barrera and Machado-Allison 1968). Interestingly, *O. albigularis* was

also abundant at this locality and frequently parasitized by *A. emarginatus*.

These data, as well as results reported in this paper, provide considerable evidence that *A. emarginatus* is host specific on species of *Oryzomys*, primarily *O. albigularis*. In this study, it was found to be restricted to *O. albigularis*, though a variety of other rodent species, which could have served as hosts, were present in sympatry with *O. albigularis*. Thus, we conclude that *A. emarginatus* is much more host specific than literature reports suggest.

In contrast to the large number of records for *A. emarginatus*, *A. tiptoni* has been reported only three times in the literature, once from Panama and twice from a single locality in Costa Rica. In the original species description of specimens from Chiriquí Province in Panama, Barrera (1966a:284) reported "long series" of *A. tiptoni* from *Peromyscus nudipes* from several localities. However, he also noted "unique material" from *Reithrodontomys creper*. The other reports of *A. tiptoni* in the literature are from Cerro de la Muerte in Costa Rica where five

specimens were reported from *Peromyscus nudipes* by Barrera (1966b), and several specimens were recorded from a single individual of *R. creper* by Vaughan (1982). In addition, we have collected *A. tiptoni* from several specimens of *Peromyscus nudipes* at Monteverde (Puntarenas Prov.) in Costa Rica (unpublished data).

The results reported here suggest that *A. tiptoni* is limited in host range to *R. creper* at the localities sampled, though relatively few specimens were collected. It was collected at only one locality and elevation range (1800–1856 m). No specimens of *P. nudipes* were found at this locality; however, *P. nudipes* was abundant at the locality where *A. emarginatus* was most common. Though this is the host of *A. tiptoni* most often reported in the literature, and the elevation is within the range known for this beetle, no beetles were found on this host.

b) Elevational zonation and host distribution.—In this study *Oryzomys albigularis* was taken at elevations above 1425 m, *Reithrodontomys creper* above 1800 m, and *Peromyscus nudipes* from 1250 to 1500 m.

In a survey of mammals from Panama, Handley (1966) reported that *Oryzomys albigularis* was an uncommon, terrestrial species found in fog forest at high elevations in both extreme eastern and western Panama. He found it at elevations ranging from 1220 to 2380 m. He reported *Reithrodontomys creper* to be abundant at high elevations in western Panama; it is primarily a terrestrial species that is found in fog forests and openings. He found it at elevations ranging from 2075 to 3175 m. *Peromyscus nudipes* was a common terrestrial species in evergreen forest. It was found at elevations ranging from 730 to 2380 m.

Oryzomys albigularis and *O. caliginosus* are widespread species in southern Central America and northern South America and are found over a range of elevations. However, *O. albigularis* is most common at higher elevations (above 1200 m), while *O. caliginosus* is most common at lower elevations (below 1000 m) to sea level (Gard-

ner 1983, Handley 1966). *Amblyopinus emarginatus* has been collected on these hosts only at elevations above 1050 m. Herein, we found *A. emarginatus* common only at 1425–1525 m elevation, and rare at 1800–1856 m elevation. Several collections were made at localities ranging from 900 to 1425 m elevation. Neither *O. albigularis* nor *A. emarginatus* were found at these lower elevations, though two other species of *Oryzomys* were present.

It is interesting that *A. emarginatus* has not been found on *O. caliginosus* in Costa Rica or Panama where *O. caliginosus* is common at lower elevations. The only report of *A. emarginatus* from *O. caliginosus* is from a single locality in Colombia where *O. albigularis* and *O. caliginosus* were sympatric at higher elevations (above 1600 m) (Barrera and Machado-Allison 1968). The occurrence of *A. emarginatus* only on *O. albigularis* in Panama (and perhaps elsewhere) may primarily be a result of the higher elevation preference of this species of *Oryzomys*. This implies that *A. emarginatus* is restricted to higher elevations, though suitable hosts occur over a much broader elevational range.

Handley (1966) reported that *Peromyscus nudipes* was common in Panama between 730 and 2380 m. However, *A. tiptoni* was collected from this species only between 1525 and 2075 m (Barrera 1966a). Barrera (1966a) reported that *A. tiptoni* was common on *P. nudipes* from numerous localities within the 1525 to 2075 m elevational range during the months of January and February. In addition, *A. tiptoni* has been collected at 3335 m from *P. nudipes* at Cerro de la Muerte in Costa Rica (Barrera 1966b) as well as at 1600 m at Monteverde (Timm, unpublished data).

In comparison, *Reithrodontomys creper* is limited to higher elevations (2075–3350 m) in the mountain systems of northwestern Panama and central Costa Rica (Hooper 1952, Handley 1966, Hall 1981). Literature reports of *A. tiptoni* from *R. creper* have been from elevations of 3200 m in Panama

(Barrera 1966a) and 3200 m in Costa Rica (Vaughan 1982). Our data indicate that *A. tiptoni* occurs on *R. creper* in Panama as low as 1800–1856 m, the lowest elevation at which this species of mammal was collected.

It is notable that 15 specimens of *P. nudipes* were collected at 25 km NNE of San Felix (1425–1525 m). This is within the elevational range from which *A. tiptoni* has been previously reported to occur on *P. nudipes*. However, no specimens of *Amblyopinus* were found on *P. nudipes* at this locality.

Conclusions

Historically, the literature on staphylinid beetles of the tribe Amblyopinini, all of which are parasitic on Neotropical mammals, has provided few specifics on the natural history and host relationships of these beetles. Our studies provide the first comprehensive data on host relationships and elevational range for a community of these beetles and potential hosts. In Central America the mammal community includes a diverse array of marsupials, edentates, insectivores, bats, primates, rodents, and carnivores. Among these potential hosts, parasitic beetles are limited to a subset of the cricetine rodents. Within a given community of cricetines, beetles appear to be restricted to one or a very few species. Specifically, our data are consistent with the interpretation that these beetles are much more host restricted than has been previously recognized.

In the communities studied, *Amblyopinus emarginatus* is host specific on *Oryzomys albigularis*. In addition, our reanalysis of distribution of *A. emarginatus* among hosts from throughout its known range provides considerable evidence of host specificity for mammals of the genus *Oryzomys* in general and *O. albigularis* in particular. The number of host records for *A. emarginatus* far exceeds those for any other amblyopinine. Therefore, though published host data for many species are confusing

and inconclusive (see for examples, Seevers 1955, Machado-Allison and Barrera 1972) our analysis of data for *A. emarginatus* provides a robust confirmation of a previously unexpected level of host specificity.

Data presented herein indicate that *Amblyopinus tiptoni* is restricted to *Reithrodontomys creper*. However, host specificity for this beetle throughout its range is less well documented. This uncertainty is partially a result of lack of comprehensive collections. Additionally, it has been reported from two species of cricetine rodents, *Peromyscus nudipes* and *R. creper*. In most instances, it has been restricted to one host locally. Considerable additional study is required to clarify host relationships of this beetle.

Additionally, our data show that while beetles of the genus *Amblyopinus* appear to be tracking specific hosts, they are restricted to that subset of the hosts' range above 1000 m. Few other groups of parasites show this restricted distributional pattern in relation to host elevational range. Wenzel and Tipton (1966) also noted that *Amblyopinus tiptoni*, as well as several other species of ectoparasites, are restricted to only a subset of their hosts' range, and suggested that these groups were primarily temperate in distribution. This implies that factors other than host range are of considerable importance to the distribution and ecology of some ectoparasites. Though factors responsible for this aspect of amblyopinine distributions are not obvious, possible candidates include temperature-humidity relationships, annual and seasonal climatic variation, and vegetational communities. This characteristic of amblyopinine ecology seems to be one of the most curious features of these beetles and merits further attention.

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Department of Zoology, Field Museum of Natural History, Chicago, Illinois 60605; (RMT) Present address: Museum of Natural History, University of Kansas, Lawrence, Kansas 66045.